Morphological diversity of stylets in *Kolhymorbis* (Mollusca: Pulmonata: Segmentinidae)

Морфологическое разнообразие стилетов рода *Kolhymorbis* (Mollusca: Pulmonata: Segmentinidae)

E.V. Soldatenko

Е.В. Солдатенко

E.V. Soldatenko, Smolensk State University, 4 Przhevalskiy St., Smolensk 214004, Russia. E-mail: sold.zoo@mail.ru

The taxonomy of freshwater pulmonates (Hygrophila) relies heavily on morphology of their reproductive system, most notably on the characters of the copulatory apparatus. For this reason, taxonomically important components of the copulatory apparatus such as penial stylets have always received much attention in the morphological studies on Hygrophila. The present study describes the stylets of *Kolhymorbis bogatovi* Zatrawkin et Moskvicheva in Zatrawkin, 1985 and *K. shadini* Starobogatov et Streletzkaja, 1967 and compares them with the previously described stylet of *K. angarensis* (Dybowski et Grochmalicki, 1925). The lengths of the stylets vary within the genus from 20 to 30 µm. In *K. bogatovi,* the stylet is a trough-shaped plate with a distal portion twisted 110° counterclockwise with respect to the proximal portion. The stylet of *K. shadini* is also a trough-shaped plate, but its walls are curved in such a way that the stylet forms a hollow cone with a beveled tip. The slit between the opposite lateral flanks of the stylet is wide proximally, but narrows down distally. The stylets of all three *Kolhymorbis* species differ markedly in their shape. The trough-shaped stylet of *K. angarensis* most likely represents the plesiomorphic state; the stylet of *K. bogatovi* may have originated from this type of stylet by increasing the curvature of the walls and counterclockwise twisting of the distal portion of the stylet. The cone-shaped stylet of *K. shadini* may have evolved from the plesiomorphic type by widening of the proximal portion and by even more pronounced curving of the walls throughout the length of the stylet without distal twisting. The penial stylets of *Kolhymorbis* species are compared with those of Palaearctic genera of the family Segmentinidae Baker, 1945 and the taxonomic utility of the stylet characters is evaluated.

В систематике пресноводных легочных моллюсков (Hygrophila) ключевыми признаками являются особенности половой системы, в частности строение совокупительных органов. Поэтому изучению стилетов как важной структуры копулятивного аппарата придается большое значение. Эта работа посвящена описанию стилетов *Kolhymorbis bogatovi* Zatrawkin et Moskvicheva in Zatrawkin, 1985 и *Kolhymorbis shadini* Starobogatov et Streletzkaja, 1967 и их сравнению с ранее описанным стилетом *Kolhymorbis angarensis* (Dybowski et Grochmalicki, 1925). Размеры структуры в пределах рода варьируют от 20 до 30 мкм. У *K. bogatovi* стилет имеет форму желобовидной пластинки с дистальным участком, повернутым против часовой стрелки на 110°. Стилет *K. shadini* также представляет собой желобовидную пластинку, но его стенки заворачиваются таким образом, что он приобретает форму полого усеченного конуса. Противоположные боковые стенки стилета не соприкасаются, образуя широкую щель, постепенно сужающуюся в дистальном направлении. Наибольшие различия между стилетами у видов рода проявляются в их форме. Исходной формой следует считать пластинчатый стилет *K. angarensis*, которой преобразуется в желобовидный стилет *K. bogatovi* путем большего заворачивания стенок и поворота дистальной части против часовой стрелки относительно продольной оси стилета. Полый усеченный конус *K. shadini* возникает из пластинчатого стилета *K. angarensis* путем некоторого расширения проксимальной части и сильного заворачивания стенок по всей длине структуры без поворота относительно продольной оси. В статье сравниваются данные по стилетам у палеарктических родов Segmentinidae Baker, 1945 и оценивается таксономическая значимость этих признаков.

Key words: freshwater molluscs, morphology, copulatory apparatus, stylet, Segmentinidae, *Kolhymorbis*

Ключевые слова: пресноводные моллюски, морфология, копулятивный аппарат, стилет, Segmentinidae, *Kolhymorbis*

INTRODUCTION

The taxonomy of freshwater pulmonates (Hygrophila) relies heavily on morphology of their reproductive system, most notably on the characters of the copulatory apparatus. For this reason, penial stylets, copulatory structures of potential taxonomic importance, have always received much attention in the morphological studies on Hygrophila (Baker, 1945; Hubendick, 1955, 1957, 1958; Odhner, 1956; Hudec, 1967; Starobogatov, 1967; Meier-Brook, 1964, 1983; Burch, 1989; Brown, 1994, 2001; Glöer, 2002; Röepstorf & Riedel, 2004; Sitnikova & Takhteev, 2006; Paraense, 2007; Soldatenko, 2009a, Soldatenko & Petrov, 2009, Soldatenko & Sitnikova, 2009; Shu et al., 2013; Soldatenko & Shatrov, 2013; Kijashko et al., 2016).

The first classification of stylets in Hygrophila was devised by Hubendick (1958) based on their external morphology. He has subdivided the stylets into three types: 1) stylets formed by condensation of penial tissues (*Physastra* Tapparone-Canefri, 1883), 2) cuticular thimble-shaped structures capping the tip of the penis (*Promenetus* F.C. Baker, 1935 and *Planorbula* Haldeman, 1840), and 3) hollow, cuticular appendages at the tip of the penis (*Anisus* Studer, 1820, *Gyraulus* Agassiz in Charpentier, 1837, and *Choanomphalus* Gerstfeldt, 1859). Meier-Brook (1983) has studied the development of the stylets in various Hygrophila and suggested that some species may also have the fourth type of penial armature that he termed plate-like stylets.

A stylet of the plate-like type as posited by Meier-Brook was first described by Soldatenko (2009a) in *Kolhymorbis angarensis* (B. Dybowski et Grochmalicki, 1925). The stylet of this species is a plate-like structure, with edges curved towards the vas deferens in its proximal portion, and completely flat in its distal portion. It could reasonably be expected that two other Far East members of the same genus: *K. bogatovi* Zatrawkin et Moskvicheva in Zatrawkin, 1985 and *K. shadini* Starobogatov et Streletzkaja, 1967, would also have penises with stylets and therefore the aim of this study was to examine the morphology of the terminal penial structures in these two species. The morphology of the stylets, however, may be significantly different in different species of the same genus, as suggested by the study of intrageneric stylet variability in a closely related family Planorbidae Rafinesque, 1815. In this family, the stylets may be almost constant in shape and length within the genus (*Anisus*) or may show considerable variability in both parameters (*Gyraulus* and *Choanomphalus*). In view of these considerations, an additional purpose of the study was to evaluate the variability of the penial armature within the genus *Kolhymorbis* Starobogatov & Streletzkaya, 1967 and compare these stylets with those of Palaearctic genera of the family Segmentinidae Baker, 1945 (= Segmentininae Baker, 1945).

MATERIAL AND METHODS

The molluscs for this study were obtained from the collections of the Zoological Institute of Russian Academy of Sciences, St Petersburg (ZISP).

Kolhymorbis angarensis (Dybowski et Grochmalicki, 1925)

Material examined. **Russia**, *Far East*: ZISP 7, 16 specimens, Primorsky Terr., Yakovlevsky Distr., vill. Varfolomeevka, temporary ponds, 25.IX.1956 (Starobogatov leg.); ZISP 11, 250 specimens, Primorsky Terr., Vladivostoksky Distr., vill. Razdol'noye, spring brook, 30.IX.1956 (Starobogatov leg.); ZISP 25, 10

specimens, Khabarovsk Terr., catchment of Amur R., bottomland of Bol'shoy In R., 19–20. VI. 1973 (Dvoryadkin leg.); ZISP 34, 15 specimens, Khabarovsk Terr., tributary of Manoma R., brook, 19.VI.1980 (Zatravkin leg.) ZISP 35, 30 specimens, Khabarovsk Terr., upper reach of Manoma R., puddle, 19.VI.1980 (Zatravkin leg.); ZISP 37, 27 specimens, Khabarovsk Terr., 10 km out a road from Komsomolsk-on-Amur, puddle, 8.VII.1980 (Starobogatov leg.); ZISP 44, 23 specimens, Khabarovsk Terr., a forest 12 km from vill. Sulukh, 12.VII.1982 (Moskvicheva leg.).

Kolhymorbis bogatovi Zatrawkin et Moskvicheva in Zatrawkin, 1985

Paratypes. ZISP 2, 29 specimens, **Russia**, *Far East*, Khabarovsk Terr., outskirts of Amursk, Bolin R. (tributary of lower Amur R.), bottomland puddle, 8.VII.1980 (Zatravkin leg.).

Kolhymorbis shadini Starobogatov et Streletzkaja, 1967

Material examined. **Russia**, *Far East*: ZISP 4, 5 specimens, Chukotka National Region, Anadyrsky Distr., Vakareva R. (channel), puddle near the camp (Anadyr expedition of 1972), 4.VIII.1972 (Streletskaya leg.)

In total, 26 individuals of the three species were dissected. Ten individuals of *K. angarensis*, three individuals of *K. bogatovi* and one individual of *K. shadini* were dissected to remove their reproductive systems for whole mount preparations. The excised structures were transferred in 70% ethanol, dehydrated in a series of alcohols, cleared in clove oil and mounted in Canada balsam. The preparations were viewed and photographed on a Leica DMLS-2 microscope equipped with a CCD camera (Fig. 1).

Copulatory organs of seven individuals of *K. angarensis*, three individuals of *K. bogatovi* and two individuals of *K. shadini* were prepared for scanning electron microscopy (SEM). The copulatory organs were excised from the molluscs and their preputia were partly or completely removed to expose the distal end of the penis with the stylet. The remaining parts of the copulatory apparatus (penis sheath, penis with the stylet and the proximal portion of the preputium) were dehydrated in ethanol, air-dried for 20 minutes in hexamethyldisilazane (Bock, 1987), coated with platinum in a HITACHI IB-5 ion sputter and viewed on a HITACHI S-570 scanning electron microscope (Fig. 2).

Of the 17 preparations of *K. angarensis* examined in this study, 10 were taken from a previous study (Soldatenko, 2009a). Since Soldatenko (2009a) did not provide detailed morphometric analysis of the stylets, these preparations were remeasured for the present study. The statistical power for the analysis of the stylets of *K. bogatovi* and *K. shadini* was limited, because the collections had only a small number of molluscs and some of the individuals in these collections had incompletely formed stylets.

RESULTS

The stylet of *Kolhymorbis angarensis*

The stylet has a length of 22.92±2.63 μm (Table 1, Lt) and is a trough-shaped plate (Figs 1a, 2a–c) slightly tapered towards its distal end or equal in width throughout its length (Table 1, Wd/Wp). The proximal end of the stylet has the greatest width (11.38±1.09 μm, Table 1, Wp) and is curved in cross section into an arc of 330–345°. Towards the mid-length of the stylet the curvature of the arc decreases to 240° and its width here is 10.43±1.09 μm (Table 1, Wm). The distal portion of the stylet is either completely flat (n=8; Fig. 2a) or its lateral corners are angled with respect to its flat middle section (n=9; Figs 1a, 2c). The portion of the stylet with curved walls comprises 0.85±0.14 of its total length (Table 1, Lc/Lt). The width of the distal end of the stylet is 8.45±1.28 μm (Table 1, Wd). The distal portion of the stylet is not twisted spirally relative to its proximal portion.

The stylet of *Kolhymorbis bogatovi*

The stylet is a trough-shaped plate (Fig. 2d–f) tapered towards its distal end or equal in width throughout its length (Table 1, Wd/Wp). The length of the stylet is

Table 1. Quantitative values (μm) and ratios for the stylets of three species of the genus *Kolhymorbis*. *n* is the number of specimens studied for each species.

Species	n	Lt	Lc	Wp	Wm	Wd	Lc/Lt	Wd/Wp
		mean±SD (min–max)	mean±SD (min–max)	mean±SD (min–max)	mean±SD (min–max)	mean±SD (min–max)	mean±SD (min–max)	mean±SD (min–max)
Kolhymorbis angarensis	17	22.92±2.63 (18.00–25.30)	19.64±4.30 (13.00–25.30)	11.38±1.09 (9.60–12.60)	10.43±1.09 (8.60–12.00)	8.45±1.28 (7.00–11.00)	0.85±0.14 (0.66–1.00)	0.75±0.12 (0.64–1.00)
Kolhymorbis bogatovi	6	23.00±3.09 (19.00–26.70)	23.00±3.09 (19.00–26.70)	13.43±1.56 (12.00–15.60)	10.67±1.25 (9.50–12.50)	8.73±2.75 (6.50–12.50)	1.00±0.00 (1.00)	0.61±0.25 (0.43–1.04)
Kolhymorbis shadini	3	25.47±2.14 (23.60–27.80)	25.47±2.14 (23.60–27.80)	13.33±3.13 (10.50–16.70)	9.77±1.97 (8.30–12.00)	5.60±0.90 (4.70–6.50)	1.00±0.00 (1.00)	0.42±0.03 (0.39–0.45)

Lc – length of stylet region with curved walls; Lt – total stylet length; Wd - distal width of stylet; Wm – stylet width at mid-length; Wp – proximal width of stylet.

23.00±3.09 μm (Table 1, Lt). The proximal portion of the stylet has the greatest width (13.43±1.56 μm, Table 1, Wp) and is curved in cross section into an arc of 160–180°. Towards the mid-length of the stylet the curvature of the arc decreases to 90° and its width here is 10.67±1.25 μm (Table 1, Wm). The distal portion of the stylet is flat, but its lateral corners are angled 15–20° with respect to the middle section. The stylet thus has either curved or angled walls throughout its length (Table 1, Lc/Lt). The width of the distal end of the stylet is 8.73±2.75 μm (Table 1, Wd; Fig. 2d–f). The distal portion of the stylet is twisted 110° counterclockwise relative to its proximal portion.

The stylet of *Kolhymorbis shadini*

The stylet of *K. shadini* is a trough-shaped plate (Fig. 1b–c), but it looks like a hollow bevelled cone, because its walls are curved in cross section into an almost complete circle and the space between the lateral edges of the stylet is covered by a cell layer (Fig. 2g–i). The slit between the opposite lateral corners of the stylet is wide proximally (6 μm), but narrows down gradually to 2 μm at the distal end of the stylet. The stylet is 25.47±2.14 μm long (Table 1, Lt) and is tapered towards its distal end (Fig. 2g–i; Table 1, Wd/Wp). The proximal portion of the stylet has the greatest width (13.33±3.13 μm, Table 1, Wp) and is curved in cross section into an arc of 330°. At its mid-length, the stylet is 9.77±1.97 μm (Table 1, Wm) wide and forms an arc of 340°. The distal end of the stylet is bevelled medially so that its middle section is shorter than the lateral flanks. The stylet is curved here in cross section into an arc of 350° and has a width of 5.60±0.90 μm (Fig. 2g–i; Table 1, Wd, Lc/Lt). The distal portion of the stylet is not twisted spirally relative to its proximal portion.

DISCUSSION

The study of the distal penial regions in *K. bogatovi* and *K. shadini* confirmed that,

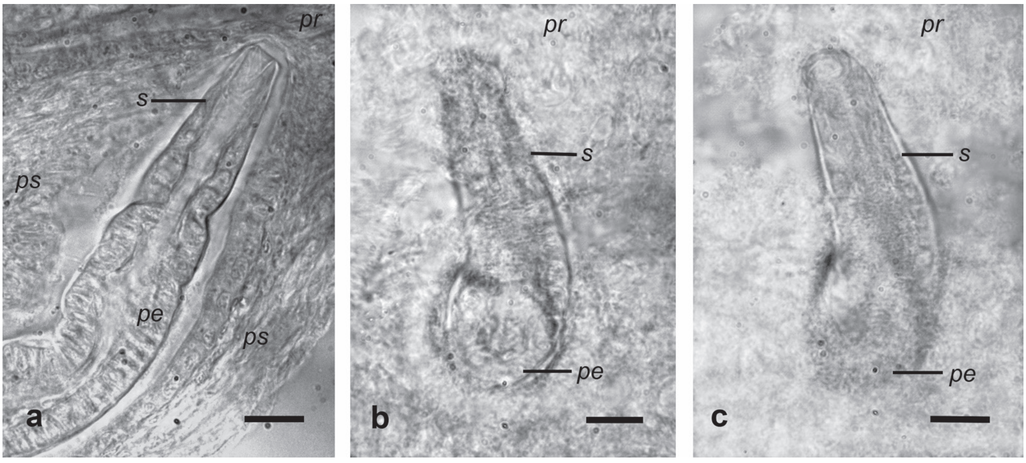


Fig. 1. Photographs of the whole mount preparations of stylets in *Kolhymorbis angarensis* (**a**) and *Kolhymorbis shadini* (**b**–**c**). Scale bars: 100 µm (**a**–**c**). Abbreviations: *pe*, penis; *pr*, preputium; *ps*, penis sheath; *s*, stylet.

like *K. angarensis*, they possess penial stylets, but the stylets of all three species have both similarities and some major differences.

A notable common trait of *Kolhymorbis* species are similar lengths of the stylets, which fall into a range from 18 to 28 µm in all three species; a somewhat greater stylet length in *K. shadini* might be explained by a bias due to a smaller sample size (Table 1). Another feature shared by all three species are curved stylet walls wrapped around the penis tip (Figs 1, 2). As the species of this genus lack penial papilla that normally provides protection for the penis tip, curved walls of the stylet might function as a protective cover for the soft penial tissues. This configuration of stylet walls may also arise from the mechanical necessity for close contact with the muscular wall of the penis to provide better leverage for the stylet movement. However, a clear understanding of the functional role of these stylets can only be obtained from studying the mechanism of copulation in the species of *Kolhymorbis*.

The most pronounced difference between the stylets is in their overall shape: a trough-shaped plate with an untwisted distal portion in *K. angarensis*, a trough-shaped plate with a twisted distal portion in *K. bogatovi* and a hollow cone with a bevelled tip in *K. shadini* (Figs 1, 2). The proximal regions of the stylets, which look essentially similar in all species, are often covered with a layer of cells, which emphasizes the differences in the shape of the stylets between the species. The width of these portions of the stylets increases from 11.38±1.09 µm in *K. angarensis* through 13.43±1.56 µm in *K. bogatovi* to 13.33±3.13 µm in *K. shadini* (Table 1, Wp). Stylets with a completely flat distal portion were found only in *K. angarensis* (Table 1, Lc, Lc/Lt). The stylet of *K. shadini* has the narrowest distal region (Table 1, Wd=5.60±0.90 µm), because of the more steeply curved walls.

The comparison of the stylet shapes within *Kolhymorbis* suggests that the trough-shaped stylet of *K. angarensis* represents the plesiomorphic state. The stylet of *K. bogatovi* may have originated by increasing the curvature of the stylet walls and counterclockwise twisting of the distal portion of the stylet. The cone-shaped stylet of *K. shadini* can also be derived from the stylet of *K. angarensis;* it may have evolved by widening of the proximal portion and by even more pronounced curving of the walls throughout the length of the stylet without distal twisting.

The proposed evolutionary scenario is also consistent with biogeographic evidence. The species with a possible plesio-

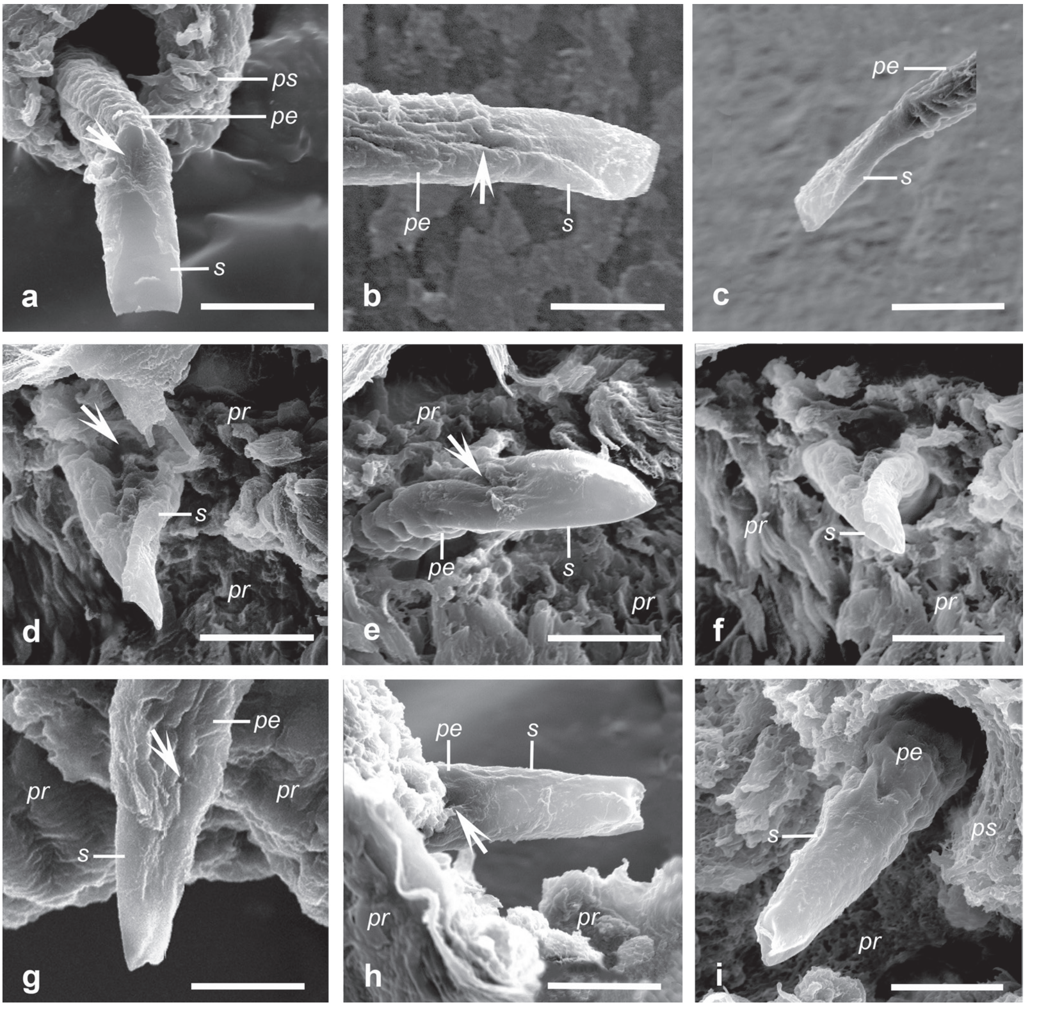


Fig. 2. SEM micrographs of the stylets of *Kolhymorbis angarensis* (**a**–**c**), *Kolhymorbis bogatovi* (**d**–**f**), and *Kolhymorbis shadini* (**g**–**i**). Scale bars: 15 µm (**a**–**i**). Abbreviations: *pe*, penis; *pr*, preputium; *ps*, penis sheath; *s*, stylet. Arrows show ejaculatory openings.

morphic type of stylet, *Kolhymorbis angarensis,* lives in Siberia, Khabarovsk Territory and Primorsky Territory (Dybowski & Grochmalicki, 1925; Starobogatov et al., 2004) and is the most widely distributed species of the genus. The species with a derived trough-shaped stylet, *K. bogatovi,* is more restricted in its distribution living in the Middle and Lower Amur (Zatrawkin, 1985; Starobogatov et al., 2004). *K. shadini,* the species with the most derived cone-shaped type of stylet, is one of the most northern species of the family; it was found along the Kolyma River and in Chukotka (Starobogatov & Streletzkaja, 1967; Starobogatov et al., 2004).

The types of penial stylet found in *Kolhymorbis* appear so far to be unique within the Segmentinidae Baker, 1945 (= Segmentininae Baker, 1945). In this family, penial stylets have been described in *Polypylis* Pilsbry, 1906 and *Helicorbis* Benson, 1855, two Asian genera closely related to *Kolhymorbis*. In *Polypylis* (*P. semiglobosa* Moskvicheva in Dworiadkin, 1980), the stylet is formed by condensation of the penial tissue,

while the stylet of *Helicorbis* (*H. shilkaensis* Starobogatov, 1996) is of the hollow type. These stylets differ from that of *Kolhymorbis* both in their shapes and the mode of formation. The representatives of the European genera *Segmentina* Fleming, 1818 and *Hippeutis* Agassiz in Charpentier, 1837, and the African genus *Segmentorbis* Mandahl-Barth, 1954 lack penial stylets entirely.

The stylets of *Kolhymorbis* show variation in shape, without any significant variability in size. This type of intrageneric variation in stylet morphology has not been previously described within the Hygrophila and is intermediate between that of the stylets of *Anisus* (Planorbidae), which are almost constant in shape and length, and that of the stylets of *Gyraulus* and *Choanomphalus* (Planorbidae), which vary greatly by both parameters. The stylets similar in shape to those of *Kolhymorbis* have not so far been described in the Hygrophila and even in the other groups of Pulmonata (Gascoigne, 1974). All three variations of the stylet in *Kolhymorbis* should be classified as a plate-like type; the defining feature of these stylets is a relatively wide (not pointed) distal region. A tubular type of stylet most closely resembling those of *Kolhymorbis* was described by Hubendick (1958) in *Gyraulus* (*Carinigyraulus*) *trapezoides* Polinski, 1929.

As the shape and size of the stylets were shown to be established early in postembryonic development and are species specific for each species (Soldatenko, 2009b; Soldatenko et al., 2011), the most important implication of this study is an emendation of the diagnosis for each of the three species studied and for the genus *Kolhymorbis* as a whole. The study of stylets can help clarify the phylogenetic relationships within the Segmentinidae and develop a more accurate taxonomic system of this family.

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